How many and which populations are necessary to maintain the viability of an ESU?

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The answer to the question 'How many and which populations are necessary to maintain the viability of an ESU?' depends on how well we can predict population dynamics within the ESU. An appropriate model of population dynamics allows us to predict persistence, the maintenance of genetic diversity and the impacts of different management strategies. An adequately predictive model can predict the viability of different population structures, allowing an estimate of which populations are necessary for viability of an ESU.

Building an adequately predictive model requires explaining the variance in demographic rates caused by fluctuations in the natural environment, density effects and management. Without an explanation of the variance in demographic rates, we must resort to 'rules of thumb' to predict the viability of an ESU. These rules can be drawn from general population or metapopulation theory, with support from selected empirical studies.

Current theory falls somewhat short of providing rules of thumb for the successful management of spatially complex populations. The predictions of general models of persistence and the maintenance of genetic variation are very sensitive to the scale of population processes like density dependence, local extinction and population mixing. Here, I offer examples of this sensitivity from theoretical studies of metapopulation dynamics and from a population viability analysis currently under development for Lahontan cutthroat trout.

A comment on how metapopulation theory applies to salmonid dynamics

Most metapopulation models bear little resemblance to salmon population dynamics. In fact, it may not be useful or prudent to think of salmon in metapopulation terms. In the original meaning of the term, 'metapopulation dynamics' referred to the extinction-recolonization dynamics that can occur when there is high correlation between individuals within the same population and low correlation between individuals in different populations. Under most metapopulation models, local persistence depends on recolonization or rescue, which is only likely when local populations experience uncorrelated dynamics.

Salmonid life-histories suggest that recolonization or rescue is not sufficient for maintaining local populations. In most salmonids, individuals within the same population are spread out over space and time, with different age classes using different environments. This strategy reduces the correlation between individuals within a population, reducing the potential for local extinction. At the same time, the dynamics of different populations can become correlated because individuals from different populations share similar ocean habitat.

Natural salmonid dynamics may have been characterized by the loss of age classes rather than whole populations. Loss of an age class allows higher persistence and maintenance of genetic diversity than loss of a population. We should be managing for natural population dynamics, assuming those dynamics are what work for the species. We should be cautious of the optimism

that salmonid 'metapopulations' can persist and maintain diversity in the face of local extinctions, when the life-history suggests alternative strategies.

Results from simple metapopulation models can illustrate the sensitivity of persistence and the maintenance of genetic diversity to population structure. Here I show results from simple metapopulation models as a caution against making 'rule-of-thumb' guidelines for persistence and diversity in complex salmonid populations.

Sensitivity of persistence and the maintenance of genetic diversity to metapopulation structure

Most metapopulation theory makes the simplifying assumption that local populations are identical in carrying capacity. But there is a continuum of metapopulation structures (Fig. 1), from many small populations to few large populations or (most commonly) populations of unequal size. In order to investigate the effect of uneven population size on the viability of metapopulations, I've explored a continuum of metapopulation structures, from even to very uneven subdivision, while holding total metapopulation capacity and number of local populations constant (Ray, in review). Along this continuum, I allow one population carrying capacity to expand at the expense of all others.

In order to make meaningful comparisons between these different metapopulation structures, I employ a defensible relationship between population size and the probability of local extinction. Models in the demographic literature (Fig. 2) commonly assume two relationships between extinction probability and population size. The probability of extinction due to demographic stochasticity, which is uncorrelated between individuals, falls off exponentially with population size, while the probability of local extinction due to environmental stochasticity, which is correlated between individuals, falls off only logarithmically with population size.

If local extinctions are completely independent and due to both demographic and environmental stochasticity, the more skewed the population size distribution the lower the persistence time of a metapopulation (Fig. 3; x axis runs from evenly subdivided metapopulations on the left to 'mainland-island' structures on the right). This conclusion is valid whenever individuals within the same population are more correlated than individuals in different populations. The stronger the relative correlation within populations, the steeper the decline in metapopulation persistence time with uneven population distribution. It may be difficult to predict the relative viability of metapopulations without a detailed understanding of the correlation between individuals within and among populations.

A similar conclusion can be drawn for the effect of population structure on the maintenance of genetic diversity. Sewall Wright illustrated that frequent local extinction can drastically reduce the genetic effective size of a population, because local extinctions cause fluctuation in total population size, decreasing the harmonic mean population size. A skewed population size distribution can exacerbate this effect. If local extinction probability falls only logarithmically with population size, then even large populations have a finite extinction probability. Metapopulations with more skewed population size distributions may exhibit lower harmonic mean size (Fig. 4; harmonic mean metapopulation size measured through generation 500; more evenly subdivided metapopulations are on the left).

However, the genetic effective size of a metapopulation can fall more rapidly than the harmonic mean size in response to skew in the population size distribution (Fig. 5; Ne at generation 500; more evenly subdivided metapopulations are on the left). The extreme sensitivity of genetic effective size to metapopulation structure is due to the fact that a skew in the population size distribution creates an opportunity for extreme variance in reproductive success. Colonists of large habitats experience much higher reproductive success than most individuals within a metapopulation suffering frequent local extinction.

So, it may also be difficult to predict the relative genetic viability of metapopulations based on simple metrics like the number and size of local populations, without data on the size distribution of local extinctions. In fact, we can't even assume that frequent local extinction will substantially reduce genetic diversity. Fig. 5 shows that the genetic effective size of an extinction-prone metapopulation can be relatively large, if the metapopulation is composed of many small and demographically independent populations.

Sensitivity of PVA predictions to unexplained variance in demographic rates and density dependence

Recent efforts to model population viability in the Lahontan cutthroat trout illustrate the sensitivity of model predictions to some common model assumptions. Often, population viability analysis consists of modeling many population trajectories by randomly choosing survival and fecundity rates from observed distributions. This approach assumes that all the variance in demographic rates is 'unexplained'; i.e., there is no relationship between survival or fecundity and the internal or environmental conditions experienced by a population. Call this Model 1. Alternatively, viability models could incorporate any relationships between demographic rates and the environment or population condition. Call this Model 2. Both approaches have been attempted with data for Lahontan cutthroat trout (Ray, Peacock and Dunham, in preparation).

The Lahontan cutthroat trout is a threatened salmonid of the Great Basin. In many portions of its range, its entire life-history is played out in small headwater streams. Most populations that are restricted to single stream habitats are found in northeastern Nevada. Among these, the population in Gance Creek stands out as potentially robust, with no significant decline since population data were first collected in 1978.

Data on the Gance Creek population includes the abundance of all age classes one through five. There are no data on fecundity. In order to parameterize Model 1, we used data on size-based fecundity from a closely related species, the West Slope cutthroat. To build Model 2, we looked for other recruitment predictors.

In this population, the number of one-year-old recruits cannot be predicted by the number of reproductive adults in the previous year. Luckily, stream flow patterns provide an excellent recruitment predictor. High spring flows may prepare spawning gravels and improve egg survival, and there is a positive relationship between spring flow in year t-1 and recruitment of one-year-olds into the population in fall of year t (Fig. 6). However, high spring flows may also flush small fish downstream into unsuitable habitats, and there is a negative relationship between

spring flow in year t and recruitment of one-year-olds in the fall of the same year (Fig. 6). A multiple regression including stream flow in years t and t-1 explains 72% of the variance in one-year-old recruitment in year t (Fig. 7). Model 2 uses this relationship, combined with stream flow data collected over the last 50 years, to predict recruitment into the future. (A minimum of 20 reproductives is assumed necessary for recruitment to occur.)

Survival rates for Model 2 are determined directly from the age-structured abundance data, as in Model 1. However, Model 2 incorporates the strong density-dependence in survival observed in most age classes (Fig. 8).

The predictions of Models 1 and 2 differ dramatically. Figure 9 shows the observed mean (square) and highest (+) and lowest (-) population sizes observed over the past two decades, as well as predictions for expected population size (and 95% confidence bounds) over the next 100 years under Models 1 and 2. Model 1 predicts the population will go extinct with nearly 40% probability within 100 years. Model 2 predicts no extinction, and predicts fluctuations over the next 100 years will be similar to fluctuations observed over the past two decades.

Model 1 was completed first, and its dire predictions set in motion a chain of events that may have been detrimental to protection of the species. Because this population is assumed to be the most robust isolated population in the region, the predictions of Model 1 raised doubts about the viability of all isolated populations in northeastern Nevada. Questions were raised about the utility of expending limited conservation resources on any of these populations.

The results from Model 2 changed the conservation strategy. Model 2 explains the variance in demographic rates in ways that allow us to explore the effects of habitat changes on population viability. For example, we can predict that lower stream flows reduce the variance in flow that is essential to recruitment. Similarly, reduced habitat capacity reduces population size through reduced (density-dependent) survival. Now the conservation strategy is to build models similar to Model 2 for all streams in the region. These models will predict which streams can support fish over the long term, and which may benefit from restored habitat and flow regimes.

Conclusion

Predictions about population persistence may be sensitive to the structure of correlation between individuals, unexplained variance in demographic rates and density dependence. Predictions about the genetic effective size of populations may be sensitive to the scale of local extinction, the scale of random mating and the potential for variance in reproductive rates. All of these data are usually difficult to obtain. Perhaps no general guidelines can be developed regarding the viability of spatially complex populations without fairly detailed models of population dynamics.

However, one aspect of spatial population structure is almost sure to convey some demographic and genetic viability: reduced environmental correlation between individuals. Even without data on critical population processes, we should manage populations in a way that will not exacerbate environmental correlations between individuals. By extension, we should probably avoid management strategies that would exacerbate a skewed population size distribution. This

conclusion has various debatable implications for the role of hatcheries in salmonid management.

References

Ray, C. Maintaining genetic diversity despite frequent local extinction: a spatial scaling problem. Submitted to Biological Conservation.

Ray, C., M. Peacock & J. Dunham. In preparation. The importance of explaining variance in demographic rates for viability modeling: an example from Lahontan cutthroat trout.
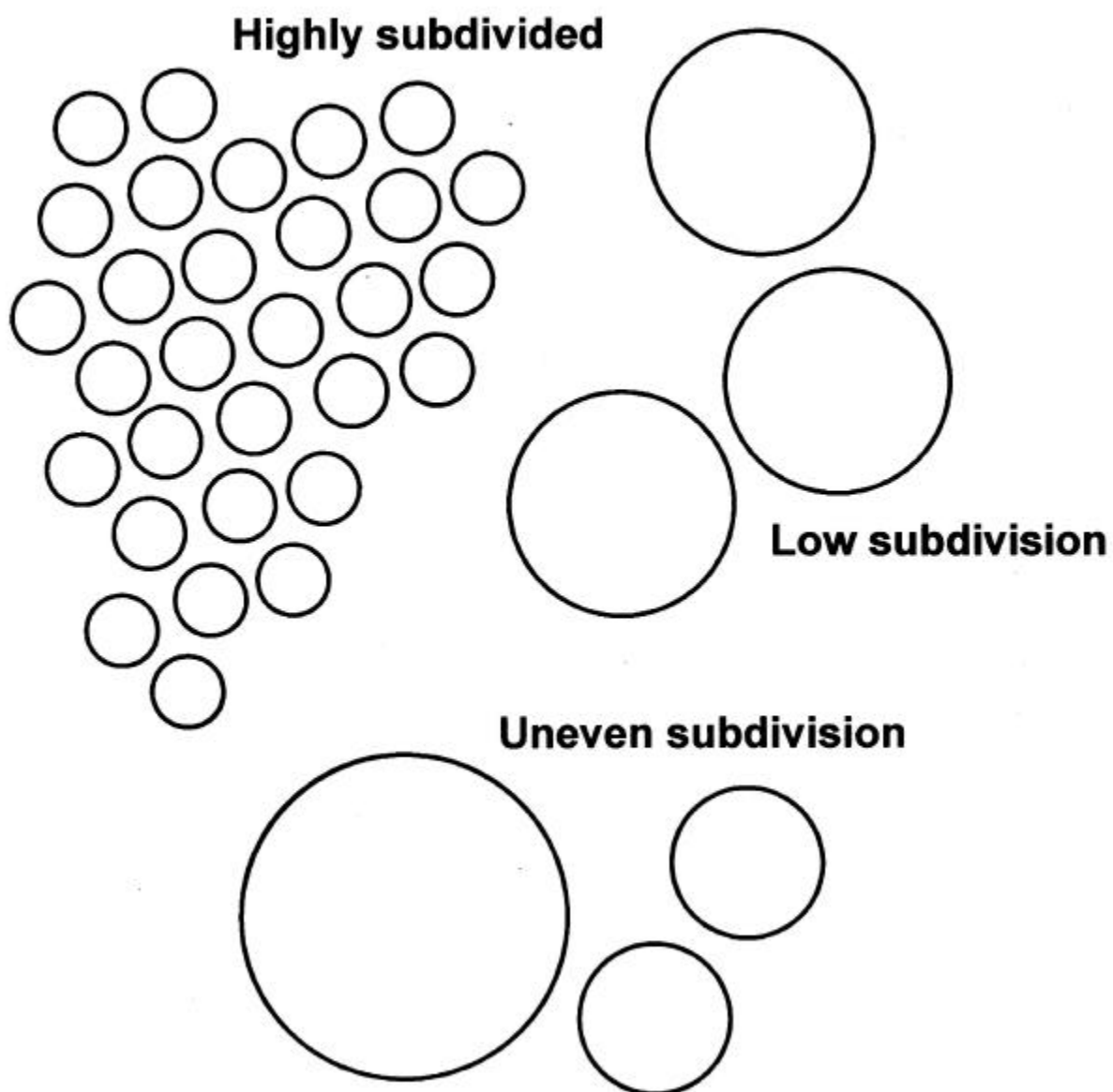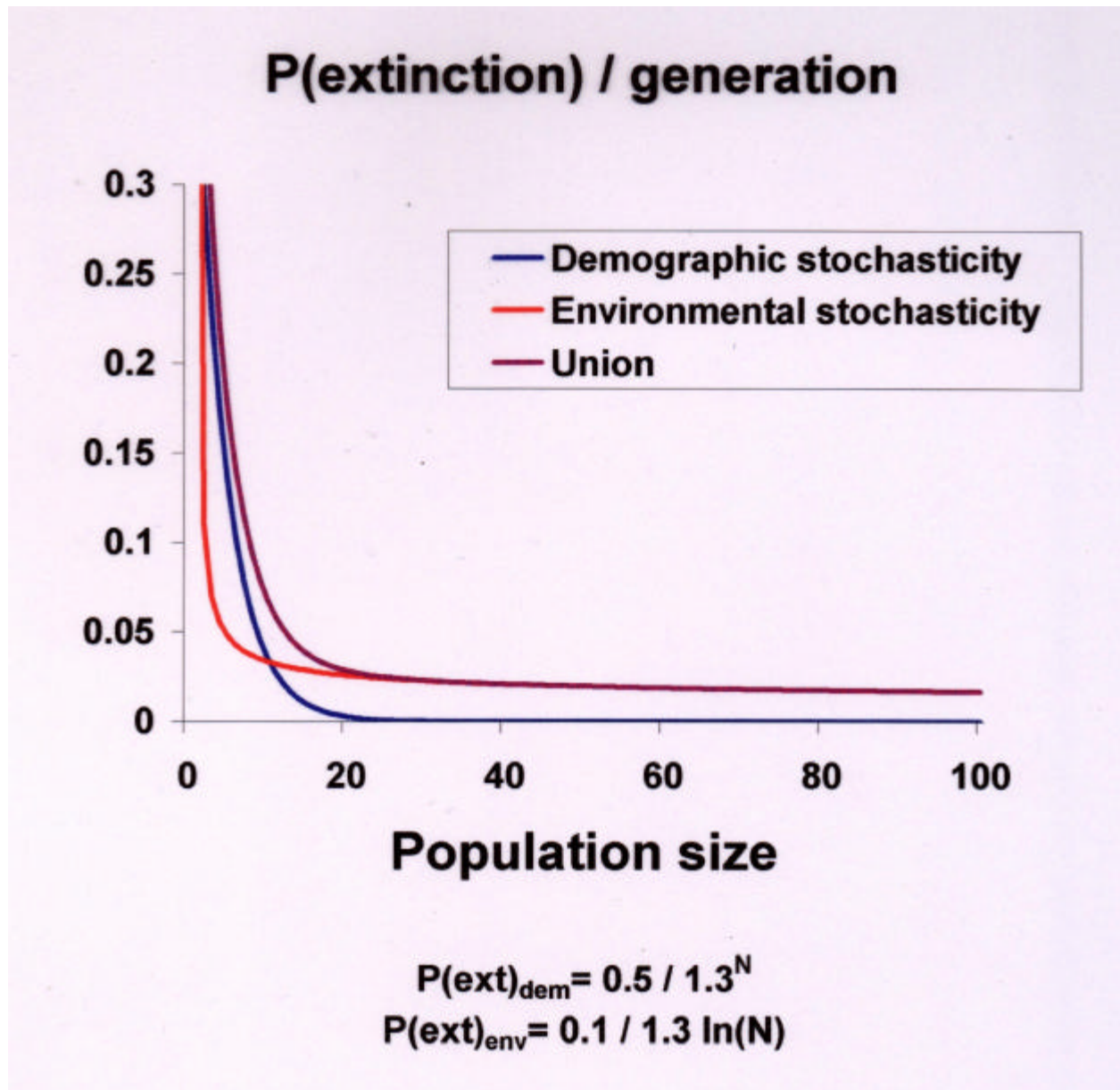
Metapopulation structures

Highly subdivided
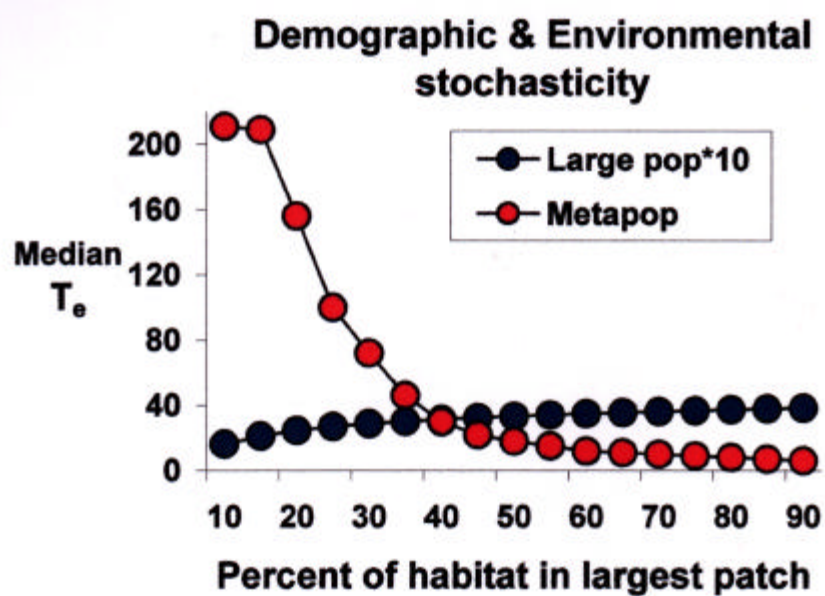
Low subdivision

Uneven subdivision

Figure 1.

P(extinction) / generation

Legend:
- Demographic stochasticity
- Environmental stochasticity
- Union

$P(ext)_{dem} = 0.5 / 1.3^N$

$P(ext)_{env} = 0.1 / 1.3 \ln(N)$

Figure 2.

Demographic & Environmental stochasticity

Legend: Large pop*10, Metapop

Y-axis: Median T_e (0, 40, 80, 120, 160, 200)

X-axis: Percent of habitat in largest patch (10, 20, 30, 40, 50, 60, 70, 80, 90)

Figure 3.

Figure 4.

N_e^{500}

20-patch metapopulations

Size of largest population: N^1_{max}

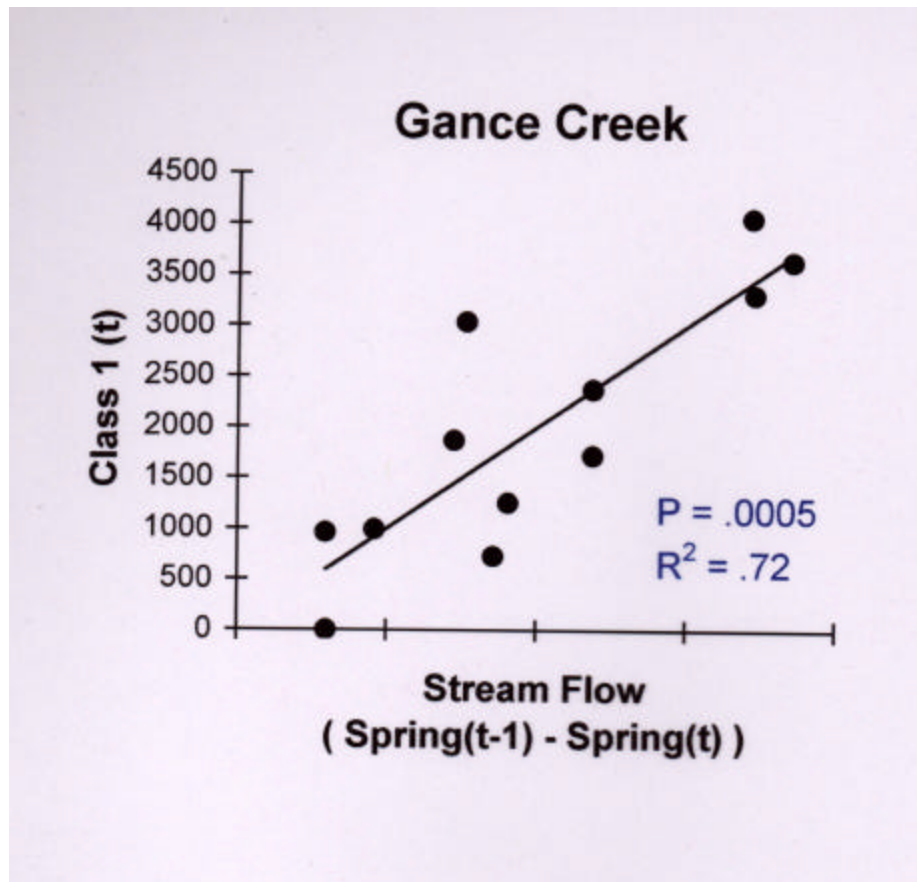$N^1_{max} + 19N_{max} = 1000$ for all metapopulations shown
Each point is an average from 500 simulations

Figure 5.

Figure 6.

Figure 7.

Figure 8.

Figure 9.